

BIOTYPES AND PHYLOGENY

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[THE substance of this paper was presented to the American Society of Naturalists at the Princeton meeting under the title "Pure Lines and Phylogeny." Dr. Johannsen entered an emphatic protest against the use of "pure line" in the sense of a group of individuals characterized by an identical combination of the same determinants. Subsequent conversation with Dr. Johannsen, and the recent clear exposition by Shull (*Science*, Jan. 5, 1912, pp. 27-29) satisfied me that what I had considered "pure lines" (such as those distinguished by Jennings in *Paramœcium*) are the pure strains called biotypes by Johannsen. I have modified my paper accordingly and have avoided using the term "pure line." I have also abandoned the very convenient term "phenotype" because my use of it as a contrast to biotype is not strictly in accord with Johannsen's usage of it as a contrast to "genotype." At Princeton, I protested against Johannsen's use of the word genotype, because the word is preëmpted for a totally different usage. I suggested a substitute, but this failed to meet with Dr. Johannsen's approval. Since I have seen Shull's definition of "genotype" (to which Dr. Johannsen himself referred me), I think the objection to the word is greater than before because "type" implies a single definite thing or model and Johannsen's "genotype" is not that but is "the fundamental hereditary . . . combination of genes of an organism." In other words it is not a concrete thing but the intangible character of that thing. It seems to me the termination "plast" (πλαστός, moulded, formed, *i. e.*, formed from

the genes) expresses the idea better than "type" (τύπος, a figure, impression, model) and "genoplast" is quite as euphonic as "genotype." The adjective form is equally satisfactory, while the use of this term will not require the abandonment of "gene." In the following pages therefore I have used "genoplast" and "genoplastic" in place of genotype and genotypical and I do not believe any misunderstanding will be possible. I have no desire to insist on these words, however. The whole matter is a very trivial one and I would very much prefer that Dr. Johannsen should himself choose a substitute for "genotype." I can not, however, agree with him that genetics and systematic zoology are so far apart that no confusion can result from using identical terms in totally different senses. I believe that so far as possible workers in any branch of biology ought to keep in touch with as much of the whole field as may be possible, and that we should all endeavor to avoid ambiguity and unintelligibility in the use of such technical terms as are necessary.—H. L. C.]

Systematic zoology and botany deal primarily with species and varieties, and can not therefore be expected to throw light upon the existence of genoplastic groups. Indeed, only those systematists who deal with organisms which reproduce asexually or parthenogenetically are likely to have any personal contact with them or even to meet with direct evidence for or against their occurrence. Since, however, the existence of such pure strains (biotypes) seems to have been definitely proved¹ the question of their relationship to the phylogenetic problems with which the systematist has to deal becomes one of some interest.

The problems of phylogeny are those of complicated polygenoplastic groups—so complicated indeed that the most complex of chemical compounds is simple in comparison. The study of these problems makes for caution

¹ JENNINGS, H. S., 1911, AMERICAN NATURALIST, Vol. 45, pp. 79–89.

in affirming that any one theory or hypothesis contains all the truth. Thus we are coming to realize that neither the Darwinian nor the De Vriesian theory of the nature of the material upon which selection works is altogether complete in itself and that neither when properly understood wholly debars the other. If we accept the current Mendelian and genoplast theories of heredity, must we not admit that all variation is fundamentally discontinuous and that what has been called continuity is not really such? It may be convenient to use such terms as "continuity" and "discontinuity" but are they not subjective ideas rather than objective realities of importance? So, too, is it necessary to claim that the genoplast theory of heredity contains all the truth and that the transmission or "phenotype" theory is wholly false? It is easy to see how in pure line breeding "ancestral influence" is, as Johannsen says, "a mystical expression for a fiction" but in the complicated polygenoplastic groups of the higher Metazoa it is hard to see why the history of the formation of a gamete may not be of importance. Is this not virtually admitted by Johannsen when he grants the existence of "perturbations by infection or contamination"? And if this be granted, why is there any necessary antagonism between the genoplast theory of heredity and the belief that "discrete particles of the chromosomes" may be "bearers of special parts of the whole inheritance"?

However this may be, none of us has any doubt that the discovery of biotypes has been a real stimulus to experimental work, and there is no reason why it may not also be a stimulus to the investigation of phylogenetic problems even though it does not assist greatly in their immediate solution. Among the difficulties of the systematist perhaps none is better known than that which we may call *the problem of large genera*—genera made up of dozens, in some cases indeed of hundreds, of species, many of which are poorly defined and more or less intergrading. Some of these genera, as *Cratægus*, *Unio* and

Salmo, have become notorious and are not infrequently referred to as proof of the futility of systematic work. Does the discovery of biotypes afford any help in explaining the existence of such genera?

I think that it does, particularly when considered in connection with the broadest interpretation of Mendel's law. If we compare one of these inclusive genera with one which contains few and well-defined species, we see that the essential difference lies in the latter having the characters sharply defined, with little diversity and no blending, while in the former the same or similar characters show so much diversity and such a tendency to blend that the resulting recombinations are most perplexing. It has occurred to me that we have here a condition of affairs analogous to what we find in the development of the individual. Certain individuals with unlike parents show what seems to be a blending of the parental characters, while in numerous other cases the characters of the individual can be referred unhesitatingly to one or the other parent. Thus, as the well-known investigations of Castle have shown, if lop-eared rabbits are crossed with rabbits having ordinary ears, the character of the ears in the offspring can not be referred to one parent rather than to the other, while if pigmented and albino rabbits are crossed, the color-character of the offspring in succeeding generations can be so referred without difficulty. This difference has been interpreted byavenport and others as due to the potencies of the determinants, the apparent blending being associated with equipotency or an approach thereto, while the distinct characters result from allelopotency. Now may it not be that a similar inequality of potency occurs among the biotypes which go to make up a species? And so when reproduction takes place we find some species in which well-defined characters are dominant and the resulting individuals form easily recognized groups, while in other species there is a lack of definiteness and a blend-

ing of characters which make the resulting forms most confusing.

Jennings has shown that there are inherent difficulties, which have so far been prohibitive, in securing crosses between biotypes of *Paramœcium* under experimental conditions, yet it is obvious that such crossing must occur constantly in nature; otherwise the whole genoplast theory becomes reduced to an absurdity. Granting then the natural crossing of biotypes, let us consider the case of a species, which for simplicity's sake we will suppose is made up of three biotypes (1, 2 and 3), each of which is distinguished by certain character-combinations, designated *a*, *b* and *c*, respectively. If the union of 1 and 2 is readily effected, while that of 1 and 3 or that of 2 and 3 rarely occurs, it is evident that *ab* will far more commonly characterize the species than *ac* or *bc* which will indeed seldom appear. The species will therefore approach identity with one of its biotypes, which may thus be considered the dominant strain. The inequipotency of the biotypes and the resulting definiteness of character in the species are obvious. If, however, the union of 1 and 3, and of 2 and 3 are as readily effected as that of 1 and 2, *ac* and *bc* will occur as frequently in the species as *ab*. In such a case the biotypes are equipotent and the resulting species may be correspondingly ill-defined.

The hypothesis here suggested of the "*inequipotency of biotypes*" may thus be the explanation of the existence of the well-defined species so generally known, while the occurrence of large heterogeneous assemblages of either species or varieties may be interpreted as due to an unusual equipotency. The experimental determination of the existence of this hypothetical difference in the potency of the biotypes within a species would well be worth while, if it should ever prove to be possible. The study of large heterogeneous groups may suggest some other lines of investigation into the nature and even the origin of biotypes. For example, such groups occur chiefly, if

not wholly, in the more specialized portion of any stock and in some cases at least appear to be associated with the fading-out or senescence of that particular branch. This suggests the possibility that the potency of a biotype ultimately alters, even though there is no visible or tangible evidence of change.

A second problem which puzzles the systematist is the *variability in the value of a character* for distinguishing species, genera and even higher groups. Color is a familiar example of this. It is of real value among birds and in numerous other cases, but is almost worthless among many invertebrates. Does the knowledge of the existence of biotypes help us to understand why this is? At first thought one might say that here again the inequity of the biotypes was the explanation of the phenomenon, but further consideration will show that this is not the case, for of course the potency of a biotype will involve all of its characteristic determinants and not merely that or those associated with the character in question. It is clear then that the value of any character for distinguishing species from each other—in other words, its value for systematic work—depends on the actual determinants in the genoplastic groups composing those species. The variability in systematic value shown by a given character is due then, not to the potency, but to *the composition of the biotypes* involved. Thus if all the biotypes contain identical color determinants, then color will be an absolutely constant character in that species, but the greater the diversity in the color determinants of the biotypes the more variable will the color of the species be and the less useful the color be as a distinguishing character. Conversely, we may say that the value of color in systematic work will depend on the degree of identity in color-determinants among the biotypes composing the species concerned. If this is so, the study of systematic characters and the measuring of their diversity may suggest some characteristics of biotypes as yet unsuspected. Thus biometrical work

even in a polygenoplastic population receives an added indorsement.

A third problem of the systematist (and for this occasion the last) is found in the fact that *diversity of morphological characters in any given species is not haphazard* or indiscriminate, but is generally restricted to such definite lines as to indicate more or less distinct stages in the phylogenesis of that species. The belief that diversity is significant and that its meaning may be discovered has received extraordinary confirmation in Jackson's just published, magnificent monograph on Echini² in which the subject is very fully discussed. An illustration taken from his work will help to make clear the desired point. In any regular sea-urchin, such as *Arbacia* or *Strongylocentrotus*, a group of ten plates surrounds the periproct, five of which are radial in position and are called oculars while the other five are interradial and are called genitals. Now in some echini all of these ten plates are in contact with the periproct and thus form a simple continuous ring but in most of the Recent species, the oculars are much smaller than the genitals and some or all of them are separated from the periproct by the meeting of adjoining genitals. In other words, some of the oculars may be excluded from the periproct and such are said to be *exsert*, while those which separate adjoining genitals and reach the periproct are called *insert*. Now Jackson has demonstrated conclusively, contrary to the widely held belief that the insertness of oculars is a matter of age and size, that for each species of sea-urchin there is a characteristic arrangement of the genito-ocular ring and that this arrangement is oftentimes a very constant character. Thus in 2,100 *Arbacias* from Woods Hole, 87 per cent. have all the oculars exsert and in more than 20,000 *Strongylocentroti* from Maine 95 per cent. have the two posterior oculars insert.

Having demonstrated the constancy of this character, Jackson has gone on to an analysis of the variations from

² Jackson, R. T., 1912. *Mem. Boston Soc. Nat. Hist.*, Vol. VII.

the normal arrangement, occurring in large series of adult specimens. And he has clearly shown that these variations are nearly always significant. There are 32 possible arrangements of the plates of the genito-ocular ring and there is no mechanical or structural reason why any one of them should not occur. If variation were perfectly haphazard every one would occur and there is no obvious reason why they might not occur, with equal frequency. Yet in fifty thousand specimens examined by Jackson, representing 137 different species of Mesozoic and Recent Echini, ten of these possible arrangements *never* occurred, and of the remaining 22 fourteen are so rare that altogether they aggregated less than $1\frac{1}{2}$ per cent. of the specimens. As a very large proportion of these were individuals abnormal in some other particular, it is fair to say that of 32 possible arrangements of the genital and ocular plates only eight (or at most ten) occur normally. Even more striking are the following facts:

When only a single ocular plate is insert, it is one of the posterior pair; this is the case in $99\frac{1}{3}$ per cent. of the specimens having one ocular insert.

When two oculars are insert, they are the posterior pair in more than 99 per cent. of the cases and in *every* case one of them belongs to that pair.

When three oculars are insert, they are the two posterior and usually the left, but sometimes the right anterior; this is demonstrated by almost 99 per cent. of the cases.

When four oculars are insert, the one exsert is invariably either the mid-anterior or right anterior.

These figures show how surprisingly definite variation is in a character which, so far as we can see, might vary with equal ease in any one of 32 ways. Yet it is only when we examine a particular case that the significance of this definiteness appears.

Jackson's work is full of such cases, but as most of us are familiar with *Strongylocentrotus*, we will consider an illustration from that genus, which, in the old, broad

sense, accepted by Jackson, includes more than twenty species. Of these some have the ambulacra relatively simple, the compound plates being made up of only four or five elements each, while in the more specialized species there may be as many as ten elements in each compound plate. The various species can be arranged roughly in a series beginning with the simplest and ending with the most specialized³ and Jackson shows that the species with the simplest ambulacra (*S. lividus*) has "no oculars insert" as the species character, with "right posterior ocular insert" as a common variant, while those with the most complex ambulacra (*S. franciscanus* and *purpuratus*) have two and often three oculars insert. Now in our common *Strongylocentrotus* from Maine, while practically 95 per cent. have two oculars insert, nearly 3 per cent. have only one insert, as in the common variant of *S. lividus*, while about 2 per cent. have three insert as in the usual variants of *S. purpuratus*. Jackson calls these *arrested* and *progressive* variants, respectively, according to whether they resemble a more simple or a more complex allied species. Whether the terminology be accepted or not, the significance of such facts can not be ignored. Are we any better prepared, with our present knowledge of the existence of biotypes, to understand the reason for this significance of variation?

If we compare a polygenoplastic group with a highly complex chemical compound, an analogy is suggested which warrants our answering this question affirmatively. In building up such a compound synthetically, the specific properties of the constituents result in the formation of certain definite compounds. These substances are necessary for the further combinations without which the ultimate compound could not be formed. In other words, the formation of the desired product is possible only because the chemical reactions

³ There are some interesting exceptions, but as they do not affect the subsequent argument, they need not be discussed here.

will take place in an orderly sequence, in consequence of the fixed specific properties of the elements involved. Now any existing species of plant or animal is a similar union of diverse elements and the possibilities of its development would seem to be limited by the same conditions which limit the formation of the chemical compound, namely, the nature of the elements and the orderly sequence of the reactions. (In either case external conditions, the environment, would make a profound difference, but for simplicity's sake we may omit reference to that influence.) As long as one believes that the elements composing a species are potentially variable in all directions, it is evident that only the pressure of external conditions can prevent an indefinite and unmeaning variety in the product. Such a belief results in making natural selection through the environment the supreme directive agent in evolutionary progress, and really puts more responsibility upon that important factor than it can reasonably be expected to bear. But as soon as it is shown that the elements involved are persistently unchanging to a remarkable degree, it becomes clear that an orderly sequence in their successive interactions will follow just as in the formation of a chemical compound. Now biotypes are the biological elements which enter into the formation of a species, and the discovery of their existence and apparent persistency makes the existence of an orderly sequence in development quite comprehensible and indicates clearly why diversity is so rarely haphazard. As in the chemical synthesis, used as an illustration, the final reaction follows necessary antecedent reactions, so in the development of the species the last step necessarily depends on the preceding, and the evolution of a group is therefore bound to be strictly linear and in definite directions. Now just as in a chemical synthesis without adding to or subtracting from its original constituent elements the process may be stopped, altered or accelerated, either by addition or removal of some substance or by

change in the external conditions, so the process of development of a species or of any of its component individuals may be arrested, altered or accelerated by similar means. Thus variants arise, individual or racial, sometimes slight, sometimes marked, but necessarily within the limits laid down by the specific properties of the biotypes involved. This may be well illustrated by one of Jackson's discoveries about variation in the genito-ocular ring of the common tropical sea-urchin, *Tripneustes*. In specimens from Florida and the West Indies, 36 per cent. have only the two posterior oculars insert, 38 per cent. have three (the left anterior plus the posterior) and 18 per cent. have four (right and left anterior plus the posterior). Evidently then individual variants both arrested and progressive are common but within very restricted limits. Further than this it appears that in Bermuda a racial variant can be distinguished, for in specimens from that locality 61 per cent. have only two oculars insert, 35 per cent. have three and only 2 per cent. have four. Now it matters not at all whether the Bermuda race is considered an arrested variant or the West Indian form a progressive variant; the important fact is the evidently marked but definitely limited racial diversity. The study of such variants, however little light it may throw on the immediate cause of their appearance, is bound to help make clear the normal line of development of the species to which they belong, and emphasizes the definiteness and the significance of their diversity. But if biotypes are really the fixed and unchanging elements which compose a species, the problem as to why this diversity is so commonly definite and significant is apparently simplified not a little by our knowledge of their existence.

It is unnecessary to suggest any other phylogenetic problems and the bearing of the study of genetics on them, for if in these which I have suggested it has not been shown that such study is helping us to understand these problems better and is even indicating solutions,

multiplication of such cases will not help the matter. Personally, I believe that the experimental work now so extensively carried on in the study of genetics is throwing a flood of light on all biological questions and that systematists not only may but must make use of the demonstrated results of such study, in attacking their own special problems, if they are really in earnest in the purpose to solve them.